



Climate-induced long-term variations in ecosystem structure and atmosphere-ocean-ecosystem processes in the Yellow Sea and East China Sea



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ABSTRACT

Located at the margin of the Northwest Pacific Ocean, the Yellow Sea (YS) and East China Sea (ECS) marine ecosystems are mainly influenced by the Kuroshio and its branches. In addition to decadal changes in their marine environments, the YS and ECS have been impacted by intensive fishing at both the species- and community-levels, leading to over-exploitation of commercial species and changes in species composition and trophic structure. The dual effects of overfishing and climate change on the variability and processes of the YS and ECS ecosystem structure and functions are not well understood. In this study, we have compiled biological and physical time series, including 147 taxa catches, 7 local-scale environmental variables and 8 large-scale climate indices, to explore variations in ecosystem structure, and to elucidate the effects of climate change on the two regions during the period 1950–2014. Aside from fishing impacts, results show that decadal variations occurred in both the YS and ECS, with step-like changes around the mid-1960s, mid-1970s, late 1980s and late 1990s. These changes correspond well with contemporaneous climatic regime shifts in the Pacific. Climate-induced changing patterns are also evident in different fish communities, with diverse sensitivities in response to these patterns. Increasing water temperature exhibits greater effects on cold-water group than on temperate- and warm-water groups. Functional and thermal groups both show pronounced linkages with fishing effort and physical drivers, particularly with local-scale environmental variables, which highlights the importance of fishing and the validity of biological grouping in future investigation of environmental impacts on marine organisms. Our results provide evidences for climate-induced variations in over-exploited marine ecosystems and coupled “Atmosphere-Ocean-Ecosystem” influencing processes, which have important implications for ecosystem-based fisheries management in the YS and ECS.

1. Introduction

Marine ecosystems have important ecological, economic and social values, contributing roughly US\$230 billion to the global economy, while supporting the livelihood of 8% of the world's population through their fisheries (Sumaila et al., 2011; Paterson et al., 2012; Strong et al., 2015).

There is increasing evidence of links between marine ecosystem variability and climate change across many regions (Wassmann et al., 2011; Wernberg et al., 2012; Barange et al., 2014; Vasilakopoulos et al., 2017). For instance, climatic regime shifts in the mid-1970s, the late 1980s and the late 1990s had major impacts on the marine ecosystem structure of the North Pacific (Overland et al., 2008). A climatic regime

shift in the mid-1970s caused an oscillation between bottom-up and top-down control and apparently contributed to the transition from an initial prey-rich ecosystem state to a final prey-poor state in the Pavlov Bay (Litzow and Ciannelli, 2007). A marine thermal regime shift in the late 1980s had large impacts on the structure of fish community in the Sea of Japan (Tian et al., 2006; 2008) and led to an ecosystem restructuring in the North Sea (Kirby et al., 2009). A major climatic regime shift of considerable ecological importance in the late 1990s resulted in shifts in pelagic and benthic feeding guild in the eastern Bering Sea and Gulf of Alaska (Megrey et al., 2009). However, because of the unpredictability of global and regional climatic regime shifts and their uncertain effects on marine organisms, major challenges remain for

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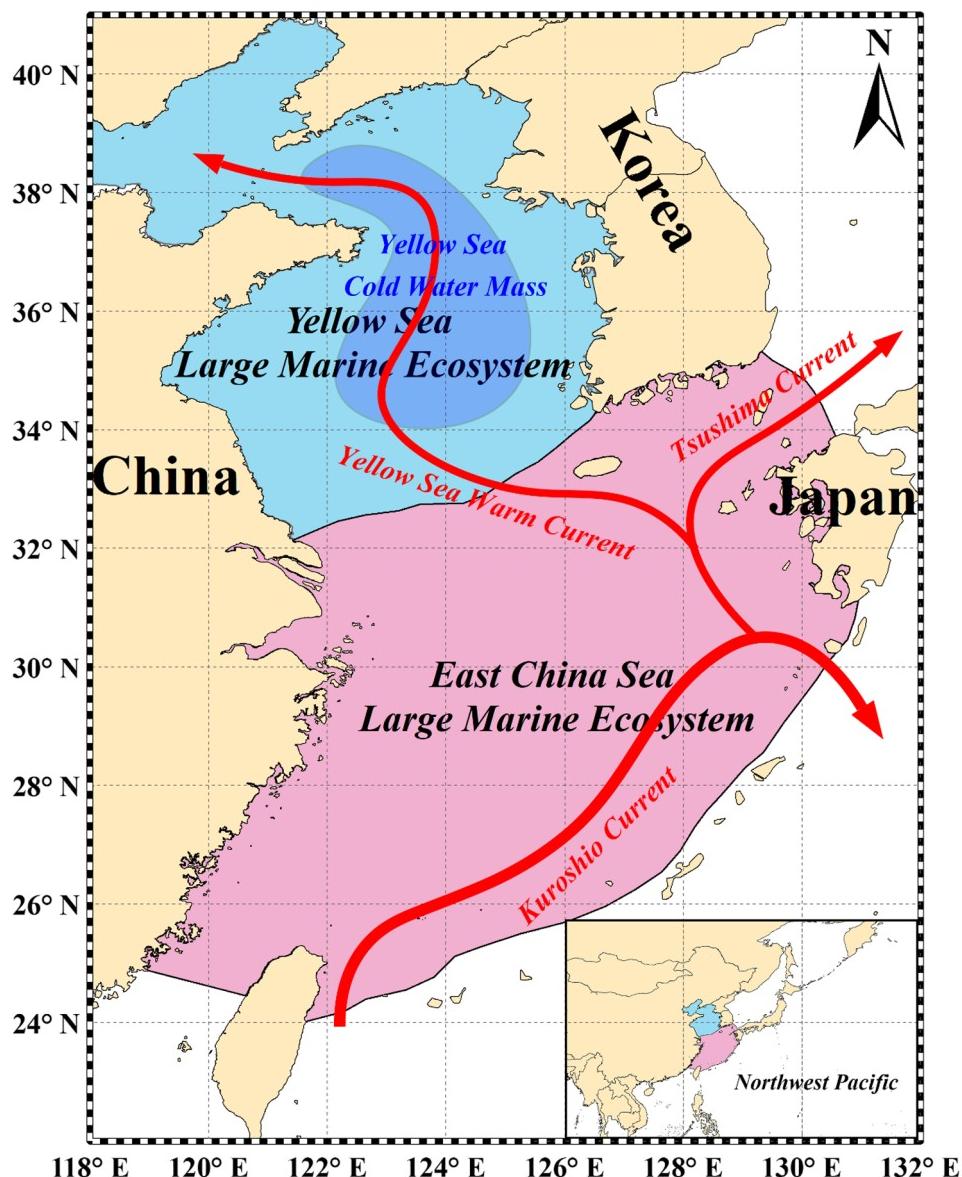


Fig. 1. Map of the research areas. Red lines represent the primary warm currents that affect the YS and ECS; the blue polygon shows the Yellow Sea Cold Water Mass that influences the YS. The panel at the bottom-right shows the location of the research areas in the Northwest Pacific. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

ecosystem management, with subsequent large effects on anthropogenic fish stock exploitations (Melnichuk et al., 2014; Arreguín-Sánchez et al., 2015).

The Yellow Sea (YS) and East China Sea (ECS) marine ecosystems are located at the western margin of the North Pacific and have important functions in the East Asian Marginal Seas (Fig. 1; Heileman and Jiang, 2009; Heileman and Tang, 2009; Jung et al., 2017). These two ecosystems undergo significant atmospheric and oceanic variability at interannual to decadal time scales driven by large-scale coupled ocean-atmosphere variability, such as the Arctic Oscillation and El Niño-Southern Oscillation (Taguchi et al., 2007; Overland et al., 2008; Liu et al., 2010; Wei et al., 2013; Cai et al., 2016). The two ecosystems also have distinguishing geographic, oceanographic, and atmospheric conditions. In particular, the YS lies in the warm temperate zone and is a semi-enclosed shelf sea affected mainly by continental high pressure system and the Yellow Sea Cold Water Mass. In contrast, the ECS lies within the subtropics, is directly open to the Pacific and is greatly affected by the oceanic low pressure system (Tang, 2009; Lui et al., 2014; Park et al., 2011a, 2011b). Furthermore, the ECS is affected by the

Kuroshio, while the YS is influenced by the Yellow Sea Warm Current, a branch of the Kuroshio (Bian et al., 2013). All the above differences may induce different variability in oceanic conditions in the YS and ECS. Previous research suggests that the changing climate has significantly impacted the physicochemical properties of seawater and would have considerable effects on marine ecosystem structure (Xie et al., 2002; Shi and Wang, 2012; Seo et al., 2014), which may also be true for the YS and ECS. However, compared to the numerous studies in other areas of the Northeast Pacific, little information regarding the effects of climate change on marine ecosystem structure of the YS and ECS is hitherto available.

The YS and ECS are among of the most productive fishery areas in the world oceans. Intense fishing pressure by Japan and Korea in the 1950s to 1970s that targeted demersal species resulted in heavy damage to demersal resources. Next, dramatically increased fishing effort by China exerted persistently high fishing pressure on the YS and ECS. Since 1989, China has become the world's largest fishery production country (FAO, 2014). Because of the heavy fishing activity over the last six decades, fisheries resources in the YS and ECS have been severely

over-exploited (Mu et al., 2007; Kleisner and Pauly, 2015). However, due to diverse biological characteristics, different species or biotic groups may give rise to different responses to over-exploitation. For example, Tang (1987) reported that the dominant species in the YS changed from small yellow croaker (*Larimichthys polyactis*) and hairtail (*Trichiurus japonicus*) in the 1950s to Pacific herring (*Clupea pallasii*) and chub mackerel (*Scomber japonicus*) in the 1970s. In addition, the proportions of Sciaenidae and Sparidae in the ECS decreased considerably since the 1960s (Otaki, 1993; Liu and Zhan, 1999). Due to ‘fishing down marine food webs’ (Pauly et al., 1998), long-lived demersal and predatory pelagic species have been replaced by lower-trophic-level species such as small pelagic fishes and invertebrates. Little research has been done on the dynamics of the ecosystem structure of the YS and ECS experiencing over-exploited status, which presents serious challenges to the managements of fisheries and associated ecosystems in Chinese waters (specifically the YS and ECS), particularly under increasingly changing atmospheric and oceanic conditions.

There is an urgent need to identify variability in marine ecosystem structure and to explore the effects of climate change, particularly considering the diverse responses of different marine organisms to changing environmental conditions. Such research is vital, not only for understanding response of ecosystem to climate change, but also for sustainable exploitation in light of climate forcing and over-exploited fishery management strategies. In this study, time series data, including fishery catch, local-scale environmental variables and large-scale climate indices have been analyzed to obtain a better understanding of the YS and ECS ecosystem dynamics in the context of climate change. The purposes of this study are: (1) To present evidence of long-term variability in the ecosystem structure of the YS and ECS; (2) to explore the effects of climate change on ecosystem structure; and (3) to discuss the possible “atmosphere-ocean-ecosystem” process that governs the YS and ECS. Results fill gaps regarding the ecosystem changes in the Northwest Pacific and contribute to the reasonable and sustainable management of ecosystems and fisheries in Chinese waters.

2. Materials and methods

2.1. Catch and biological data

Catch data, including discards and unreported portions from surrounding countries around the YS and ECS from 1950 to 2014, were obtained from the Sea Around Us project (<http://www.searoundus.org/>; Pauly and Zeller, 2016). Catch data for each taxon (species to class) from all fishing entities, fishing sectors, catch types and reporting status were integrated by year to explore interannual to decadal variations. Catches were identified to different taxonomic levels including species, genus, family, order and class. Catches that were identified to the genus and family levels were generally dominated by species that had similar biological characteristics and similar responses to environmental conditions. In addition, catches at the levels of order (all were invertebrates) and class were relatively low, which would have little effects on analyses that focus on climate-induced variations in ecosystem structure rather than specific species. Therefore, the different taxonomic resolutions among the taxa would result in negligible effects on subsequent analyses. The selected YS catch data set consists of 66 taxa, including 41 species, 8 genera, 12 families, 3 orders and 2 classes, accounting for 64.66% of the total catch in the YS (Supplement Table S1; Supplement Fig. S1). The selected ECS catch data set consists of 81 taxa, including 56 species, 7 genera, 13 families, 3 orders and 2 classes, accounting for 70.05% of the total catch in the ECS (Supplement Table S2; Supplement Fig. S1). The trophic level and optimal temperature (median value in the optimal temperature range) for each taxon were derived from Sea Around Us and previous research (Cheung et al., 2013; Liang et al., 2018), respectively. All taxa were classified into functional groups, specifically, the large predatory group, small pelagic group, demersal group and invertebrates, according to their trophic

levels, biological characteristics and previous studies (Tian et al., 2006, 2013b). The taxa were also classified into three thermal groups (warm-water, temperate-water and cold-water groups) according to their optimal temperature, with the warm-water group having optimal temperatures greater than or equal to 25 °C and cold-water less than or equal to 15 °C. Considering that mean water temperatures have risen from 14.5 to 15.5 °C in the YS and from 23.5 to 24.5 °C in the ECS, including taxa with optimal temperatures ranging from 16 to 24 °C into the temperate-water group would be inaccurate, as their wide range of optimal temperatures may mitigate or weaken the effects of thermal variability. Furthermore, the temperate-water group needs to be adjusted according to the different thermal conditions between the YS and ECS. Therefore, taxa with optimal temperature ranging from 16 to 20 °C and from 20 to 24 °C were regarded as temperate-water in the YS and ECS, respectively. Details are shown in Supplement Table S1 for the YS and Supplement Table S2 for the ECS.

Engine power data for the total number of Chinese marine fishing boats in the YS and ECS were derived from Chinese Fishery Statistics from 1950 to 2014 to represent fishing efforts in these two areas (Zhao et al., 2015). In addition, fishing effort data for Japanese and Korean fishery in the YS and ECS were collected from Cheng et al. (2006) to provide reference for our results (Supplement Fig. S2).

2.2. Local-scale environmental variables

Sea surface temperature (SST), sea surface salinity (SSS), sea level pressure (SLP), scalar wind (SW), wind direction (WD), air temperature (AT), and precipitable water content (PWC) were chosen to illustrate local environmental changes in the YS and ECS (Xie et al., 2002; Park et al., 2011a, 2011b; Cheng et al., 2015; Wei et al., 2015; Zheng et al., 2015). All environmental variables were derived from open-access online monthly databases for the period 1960 to 2014. It has been reported and extensively explored that variations in the winter average of local-scale environmental variables, as well as winter averages of large-scale climate indices, have strong linkages with variations in various ecological processes (Overland et al., 2008; Alheit and Bakun, 2010). Therefore, winter (January-March, is most frequently used in research regarding Chinese waters) averages for each variable were calculated to effectively represent variations in environmental conditions (Xie et al., 2002). Chlorophyll-a concentration and dissolved oxygen were not included in our study due to a lack of relevant data. Detailed descriptions and sources are provided in Supplement Table S3.

2.3. Large-scale climate indices

The Pacific Decadal Oscillation (PDO) index, North Pacific Gyre Oscillation (NPGO) index, Arctic Oscillation Index (AOI), Pacific-North America (PNA) index, North Pacific Index (NPI), Southern Oscillation Index (SOI), East Asian Monsoon (MOI) and Sea Surface Temperature (SST) in Niño 4 Region (Niño 4) were used to define climate change in the North Pacific. All indices were derived from open-access online monthly databases for the period 1950 to 2014. These large-scale climate indices are well-documented and largely associated with variations in the North Pacific fish communities and ecosystem (Di Lorenzo et al., 2008; Alheit and Bakun, 2010; Tian et al., 2013a; Tu et al., 2015). Particular large-scale climate processes, such as the Aleutian Low, Arctic Oscillation and Asian Monsoon are most active in winter. Therefore, winter (December-February, is most frequently used in relevant research) averages for each index were calculated to represent variability in large-scale climate indices and to correspond to variability in local-scale environmental variables. Although there is a one month lag between local-scale environmental variables and large-scale climate indices, this lag has negligible effects on our results at interannual to decadal time scales. Data descriptions and sources are provided in Supplement Table S4.

2.4. Calculating surrogates for ecosystems

Principal component analysis (PCA) was used to identify the most important patterns of common variability in each data set (Hare and Mantua, 2000). Prior to PCA, missing values in the catch data (2.68% of the YS and 2.36% of the ECS) were estimated using multiple imputation with Bayesian linear regression techniques (Buuren and Groothuis-Oudshoorn, 2011). Multiple imputation was conducted using the “mice” procedure (mice package) in R (R core Team, 2018), with each imputed value derived from five iterations and each iteration consisting of 100 imputations. PCA was then applied to the imputed catch data for the YS and ECS, local-scale environmental variables for the YS and ECS and large-scale climate indices, respectively. The number of principal components (PCs) for each data set was determined by a combination of the Kaiser-Harris criterion, the Cattell scree test and Parallel analysis (Humphreys and Montanelli, 1975; Velicer, 1976). PCs scores were considered surrogates of each data set for further analyses. Only the first two PCs for catch data set (PC_{bio} s) were retained so as to focus on the most important modes of variability in ecosystem structure (Litzow et al., 2014). The mean PC_{bio} scores and associated standard deviation (SD) for each year with missing values were estimated from the distribution of the 100 imputed values. In addition, we interpreted the variability captured by PCs in terms of the strongest time series loadings (absolute loading values $P \geq 0.3$ for large-scale climate indices PCs, $P \geq 0.4$ for environmental variables PCs, and $P \geq 0.15$ for catch data PCs) (Litzow and Mueter, 2014). Analyses were conducted by the “prcomp” and “fa.parallel” procedures (psych package) in R (R Core Team, 2018).

The mean trophic level (MTL) of catch is an indicator of the sustainability in exploited marine ecosystems and of variations in ecosystem structure with its integrative nature (Pauly et al., 2002; Cury et al., 2005). Here, we used MTL to represent the variations in ecosystem structure of the YS and ECS. In addition, the mean temperature of catch (MTC) was calculated to assess potential effects of climate change (Cheung et al., 2013). The MTL and MTC are defined as follows:

$$MTLy = \frac{\sum_i^n Ci, yr \times TL_i}{\sum_i^n Ci, yr} \quad (1)$$

$$MTCyr = \frac{\sum_i^n Ci, yr \times Ti}{\sum_i^n Ci, yr} \quad (2)$$

where $C_{i,yr}$ is the catch of species i in year yr , TL_i and T_i are the trophic level and optimal temperature of species i , and n is the total number of species.

2.5. Regime shift detection

The sequential t-test analysis of regime shift (STARS) developed by Rodionov (2004) was applied to detect trends and regime shifts in the derived PCs, MTLs and MTCs. Because of the presence of autocorrelation in the time series, we used a “prewhitening” procedure before applying the STARS algorithm (ver.3) (Rodionov, 2006). STARS results are determined by the cut-off length for proposed regimes (L) and the Huber weight parameters (H), which defines the range of departure from the observed mean beyond which observations are considered as outliers (Thomson and Emery, 2014). Following exploratory analyses with STARS, L was set to 10 and H to 1, with a significant level of 5%. STARS was written in Visual Basic for Application (VBA) for Microsoft Excel and was available at www.BeringClimate.noaa.gov (Rodionov, 2004; Rodionov and Overland, 2005).

To assist visualizing the trends in the time series of PCs, the cumulative sum (CuSum) was calculated by the simple addition of a datum to the sum of all previous data points, as what was done in Beamish et al. (1999) and Tian et al. (2004).

Chronological cluster analysis was applied to the imputed catch data

for the YS and ECS, local-scale environmental variables for the YS and ECS, and large-scale climate indices to identify temporal breaks related to regime shifts. Chronological cluster analysis is a type of constrained cluster analysis that takes into account the temporal characteristics of multivariate data collected over time and has been used successfully in the identification of regime shifts in multivariate ecological and environmental data (Legendre et al., 1985; Hare and Mantua, 2000; Weijerman et al., 2005) and in temporal shifts in fish community structure (Galzin, 1987; Kirkman et al., 2015). In this study, chronological clustering was performed using multivariate regression tree analysis (MRT) (De'ath, 2002), which is an extension of the univariate regression tree analysis intended for multivariate response variables. Here, year (yr) is the explanatory variable, and the output of the MRT is a tree with leaves (also known as terminal nodes), each of which represents a subset of the explanatory variable that minimizes the within-group sums of squares. Details of the algorithm and model selection procedures are provided in De'ath (2002) and Borcard et al. (2011). In addition, the sensitivity of the results to the number and type of time series included was assessed by conducting 1000 permutations for x number of randomly chosen time series, with the value of x ranging from 1 to the total number (n) of time series (e.g., 1, 2, 3, ..., 8 for large-scale climate indices). The results were presented as histograms showing the frequency with which each year was selected as a regime shift for each value of x . Chronological cluster was conducted using the “mvp” procedure (mvp package) in R available online at: <http://ftp.auckland.ac.nz/software/CRAN/src/contrib/Descriptions/mvp.html>.

2.6. Relationships among ecosystem, environment and climate

Pearson correlation analysis was used to detect linear correlations among PCs for catch data (PC_{bio} s), PCs for local-scale environmental variables (PC_{env} s) and PCs for large-scale climate indices (PC_{cls}) (Hare and Mantua, 2000). In addition, correlation analyses were applied to PC_{cls} , PC_{env} s and fishing effort to test the dependence between physical drivers and fishing activity. The number of degrees of freedom of coefficients obtained from significance tests were adjusted based on the potential autocorrelation in the PCs and fishing effort according to the methods of Bretherton et al. (1999). Analyses were conducted using “corr.test” procedure (psych package) in R (R Core Team, 2018).

Gradient forest analysis was employed to further quantify the relationships between biological data (including ecosystem surrogates of PC_{bio} s, MTL, and MTC as well as time series of functional and thermal groups) and predictors/drivers (including fishing effort and physical drivers of PC_{env} s and PC_{cls}). The gradient forest method is built upon random forests to capture complex relationships between potentially correlated predictors and multiple response variables by integrating individual random forest analyses over the different response variables (Ellis et al. 2012). In essence, random forests are regression trees that partition the response variable into two groups at a specific split value for each predictor p to maximize homogeneity. Along with other measures, gradient forests provide the goodness-of-fit, R_f^2 , for each response variable f and the importance weighted by R_f^2 . In this study, we ran the gradient forests 1000 times to obtain the variability of R_f^2 . The run with the highest overall performance (R^2) was then used for further analyses. Analyses were conducted using the “gradientForest” package available, online at <http://gradientforest.r-forge.r-project.org/>.

3. Results

3.1. Variability in the YS and ECS marine ecosystem structure

The first two PC_{bio} s account for 59.77% and 55.38% of the catch data variance for the YS and ECS, respectively (Supplement Fig. S3). YS PC_1 _{bio} better captures the variability in relatively warm-water and high-trophic-level taxa than does YS PC_2 _{bio} and is characterized by intensive negative

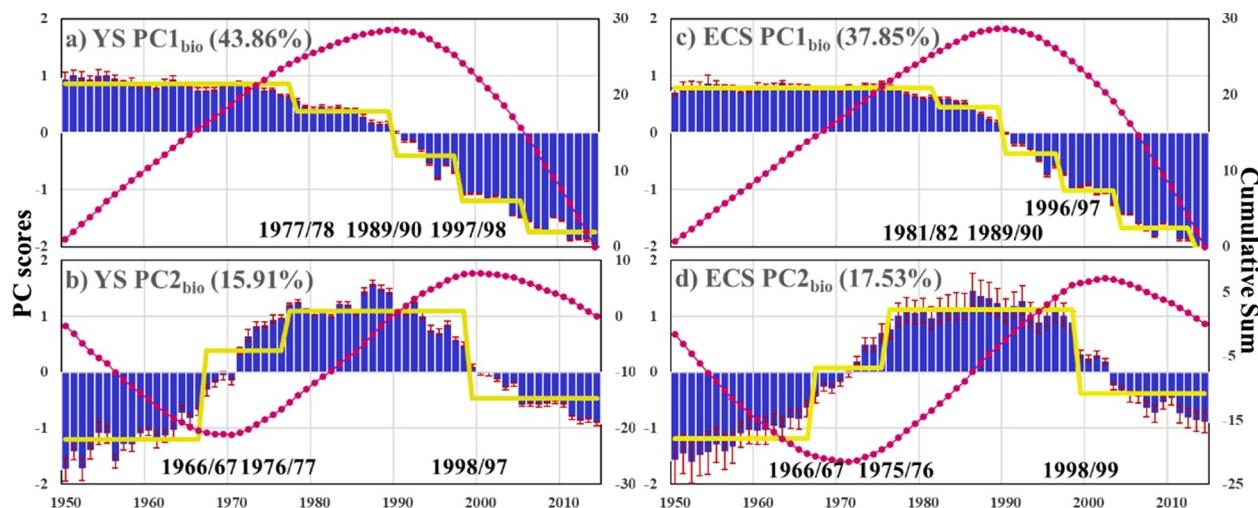


Fig. 2. PC scores of: (a) The YS PC₁_{bio}, (b) the YS PC₂_{bio}, (c) the ECS PC₁_{bio} and (d) the ECS PC₂_{bio}. Blue bars represent scores, red lines with symbols represent cumulative sums for scores and yellow lines represent regime means detected by STARS. Error lines show standard deviations estimated using 100 PC scores that are generated by 100 imputed data sets. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

loadings (Supplement materials; Supplement Figs. S4a, S5a, c), while YS PC₂_{bio} represents variability in temperate-water and relatively low-trophic-level taxa and has predominantly positive loadings (Supplement Figs. S4b, S5b, d). YS PC₁_{bio} reveals a decreasing trend since the late 1970s, characterized by a decadal pattern with step-like changes in 1977/78, 1989/90 and 1997/98, and YS PC₂_{bio} had step-like changes in 1966/67, 1976/77 and 1998/99 at the decadal to multi-decadal scales (Fig. 2a, b). ECS PC₁_{bio} captures variability in warm-water taxa with no apparent trophic-level pattern and loadings are all negative (Supplement Figs. S4c, S6a, c). ECS PC₂_{bio} is indicative of warm-water and relatively high-trophic-level taxa with almost all positive loadings (Supplement Figs. S4d, S6b, d). ECS PC_{bio}s are similar to YS PC_{bio}s with step-like changes in 1981/82, 1989/90 and 1996/97 for PC₁_{bio}s and in 1966/67, 1975/76 and 1998/99 for PC₂_{bio}s (Fig. 2c, d).

Time series of functional groups in the YS and ECS show similar characteristics except for a great enhanced small pelagic group in the ECS from the mid-1970s to the late 1980s, which reduced the proportions of demersal species and invertebrates in this ecosystem (Fig. 3a, b). Thermal groups in the YS and ECS have similar patterns in terms of a

generally decreasing trend in the cold-water group and increasing trend in the warm-water group (Fig. 3c, d). However, the ECS has been dominated by the temperate-water group throughout the entire time period while the YS was composed of nearly 40% cold-water group prior to the decline after the mid-1970s.

The YS MTL decreased until the early 1990s and then stabilized after the late 1990s with step-like changes in 1963/64, 1974/75, 1985/86 and 1993/94 (Fig. 4a). The ECS MTL showed apparent staged variations with step-like changes in 1975/76 and 1992/93 (Fig. 4b). The YS MTC remained steady until the mid-1970s and then increased until the early 1990s with step-like changes in 1976/77 and 1993/94 (Fig. 4c). The ECS MTC increased from the early 1960s to the late 1970s, decreased in the early and mid-1990s and then increased in the late 1990s with step-like changes in 1966/67, 1976/77 and 2003/04 (Fig. 4d).

Chronological cluster results highlight the step-like changes in the YS catch data in 1966/67, 1977/78, 1989/90 and 2002/03 (Fig. 5a), and the step-like changes in the ECS catch data in 1980/81 and 2002/03 (Fig. 5b). All of the time nodes are characterized by high stability

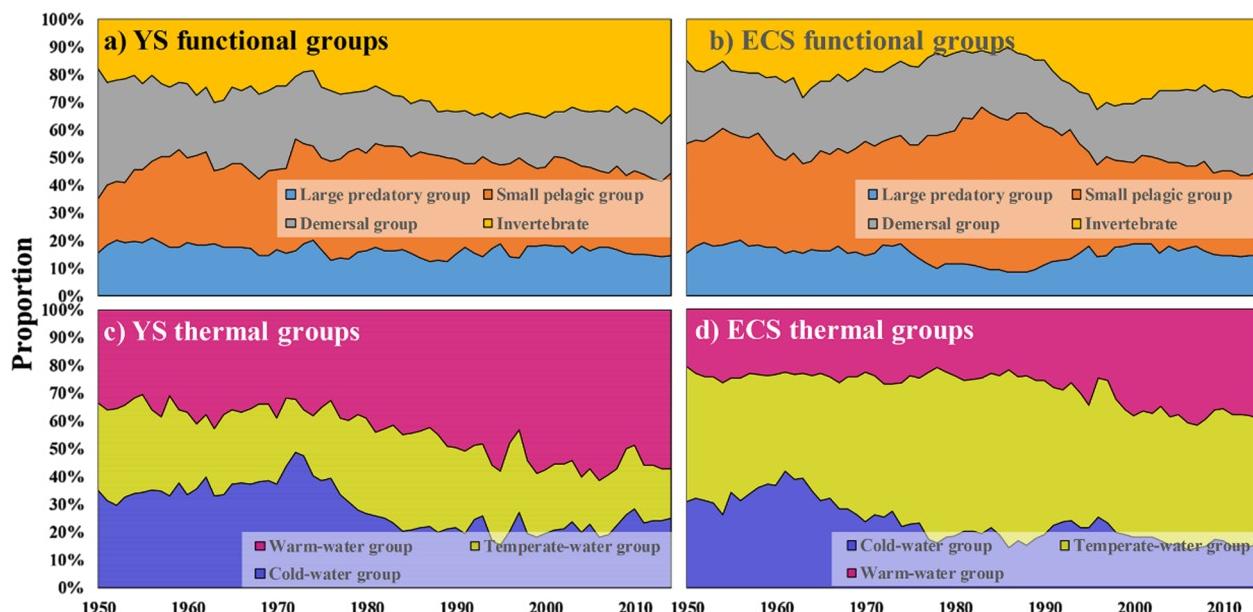


Fig. 3. Variations in catch proportions of: (a) The YS functional groups; (b) the ECS functional groups; (c) the YS thermal groups and (d) the ECS thermal groups.

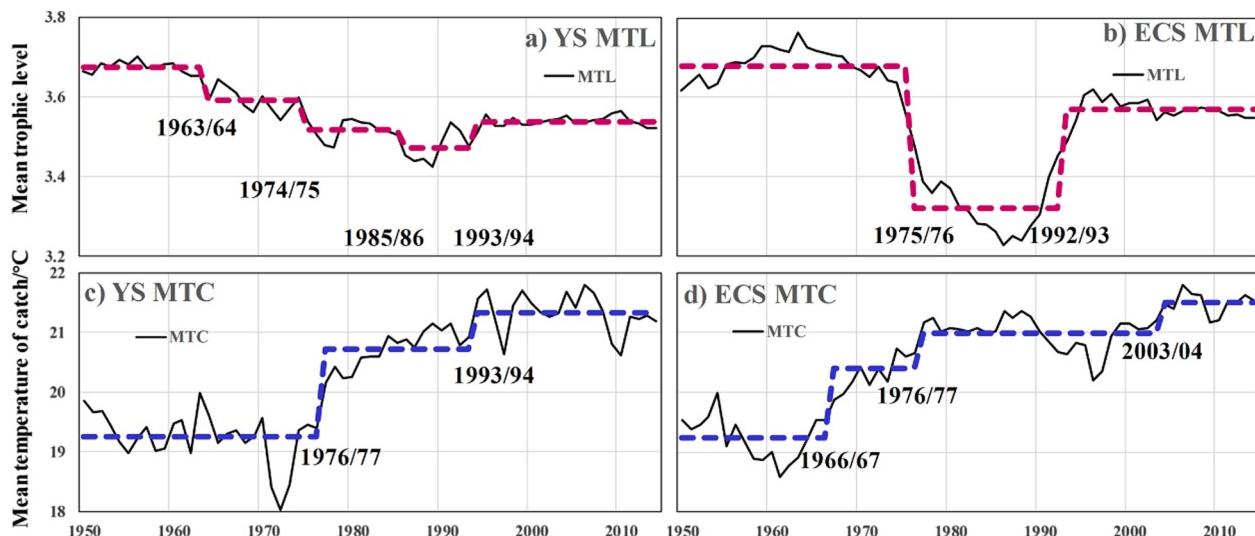


Fig. 4. Variations in: (a) The YS MTL; (b) the ECS MTL; (c) the YS MTC and (d) the ECS MTC. Dotted lines represent regime means detected by STARS. MTL: mean trophic level, MTC: mean temperature of catch.

and have significantly higher frequency than other time nodes in almost all sample sizes.

3.2. Local-scale environmental changes in the YS and ECS

The first three PC_{ev}s account for 71.96% of the total variance in the local-scale environmental variables in the YS (Supplement Fig. S7a). YS PC1_{ev} captures patterns in SST and AT (thermal variability), explaining 32.13% of the total variance; YS PC2_{ev} represents variations in SLP and WD, explaining 22.34% of the variance; while YS PC3_{ev} characterizes variations in SSS and PWC, accounting for 17.41% of the variance (Supplement Fig. S8a). The three YS PC_{ev}s reveal regime shifts in 1987/88, 1981/82 and 1998/99, respectively (Fig. 6a–c). The first two PC_{ev}s of the local-scale environmental variables in the ECS have a cumulative explanation of 60.45% of the total variance (Supplement Fig. S7b). ECS PC1_{ev} captures variability in SST, AT and PWC, for a total accounting of 42.21% and ECS PC2_{ev} captures variability in SLP and SW for a total accounting of 18.84% (Supplement Fig. S8b). ECS PC1_{ev} shows regime shifts in 1987/88 and 1997/98, while ECS PC2_{ev} has one shift in 1982/83, with another potential one in 2010/11 that needs to be verified using longer time-series (Fig. 6d, e). In all, local-scale environmental variables in the YS and ECS show regime shifts in the early 1980s, the late 1980s and the late 1990s.

Chronological cluster results highlight the regime shifts in 1987/88 and 1998/99 in the YS and in 1987/88 in the ECS (Fig. 7). All the time nodes are characterized by high stability with significantly higher frequency than other time nodes in almost all sample sizes. In addition, the results verify the climatic regime shifts in the late 1980s and the late 1990s.

3.3. Large-scale climate change in the North Pacific

The first three PC_{ci}s of the large-scale climate indices account for a cumulative explanation of 79.94% of the total variance, which well represents the large-scale climate change in the North Pacific (Supplement Fig. S7c). PC1_{ci} captures variability in PDO, PNA, NPI, SOI and Nino 4 with an explanation of 43.38%; PC2_{ci} represents variability in AOI, SOI, MOI and Nino 4 with an explanation of 21.01% and PC3_{ci} captures variability in NPGO, AOI and MOI with an explanation of 15.55% (Supplement Fig. S8c). Respective regime shifts for the three PC_{ci}s occurred in 1976/77 and 2007/08, 1988/89 and 1998/99, and 1997/98 (Fig. 8). Correspondingly, climatic regime shifts in the North Pacific appear to have occurred in 1976/77, 1988/89 and late 1990s,

with significant decadal pattern. A possible regime shift in 2007/08 can only be determined with longer time-series.

Chronological cluster results highlight the climatic regime shifts in the North Pacific in 1976/77 and 1986/87, with a probability of over 0.3 (Fig. 9). All of the time nodes are characterized by high stability, with significantly higher frequency than other time nodes in almost all sample sizes.

3.4. Relationships among climate, environment and ecosystem

Ecosystems surrogates of the YS and ECS underwent step-like changes in the mid-1970s, the late 1980s and the late 1990s, corresponding closely with regime shifts in large-scale climate indices in the mid-1970s, the late 1980s and the late 1990s, and with regime shifts in local-scale environmental variables in the late 1980s and the late 1990s (Table 1). However, the regime shifts in the mid-1960s in the YS and ECS catch data were not accompanied by any shifts in the environmental variables and climate indices. The YS and ECS PC1_{bio}s are significantly correlated with PC1_{ev}s and PC3_{ev}s of the YS and PC_{ev}s of the ECS, respectively (Table 2). However, none of the PC_{bio}s has correlations with the PC_{ci}s. For both the YS and ECS, local-scale environmental variables (mainly PC1_{ev}s) show significant relationship to large-scale climate change associated with PC2_{ci} and PC3_{ci} (Table 3), indicating that environmental changes in the YS and ECS are largely affected by the MOI and AOI (the variability is captured by PC2_{ci} and PC3_{ci}). In addition, fishing effort in both the YS and ECS are correlated with PC_{ci}3 as well as PC1_{ev} and PC3_{ev} of YS and PC1_{ev} and PC2_{ev} of ECS, respectively (Table 4).

Gradient forest analyses identify the dominant importance of fishing effort (YS_{fe} and ECS_{fe}) as predictors for variations in ecosystem structure, while local-scale environmental variables contribute relatively less to ecosystem surrogates of the YS and ECS (Supplement Fig. S9). In addition, climate indices contribute least as predictors for both the YS and ECS except for PC1_{ci} for the YS (Supplement Fig. S9). For both the YS and ECS, the variations in PC1_{bio} are best explained by the predictors with the highest R², followed by the MTC with a R² of around 0.8 (Fig. 10). In addition, PC1_{bio}s indicate strong threshold responses to positive fishing effort YS_{fe} and ECS_{fe}, respectively (Fig. 11). By contrast, the MTCs have strong threshold responses to negative fishing effort. In the YS, PC_{bio}s also have strong threshold responses when YS PC3_{ev} is around -1.0 to -0.5 (Fig. 11a); and in the ECS, PC1_{bio} and MTC have threshold responses when ECS PC2_{ev} is around -1 to -0.5 (Fig. 11b).

Time series of the functional groups have markedly quite different

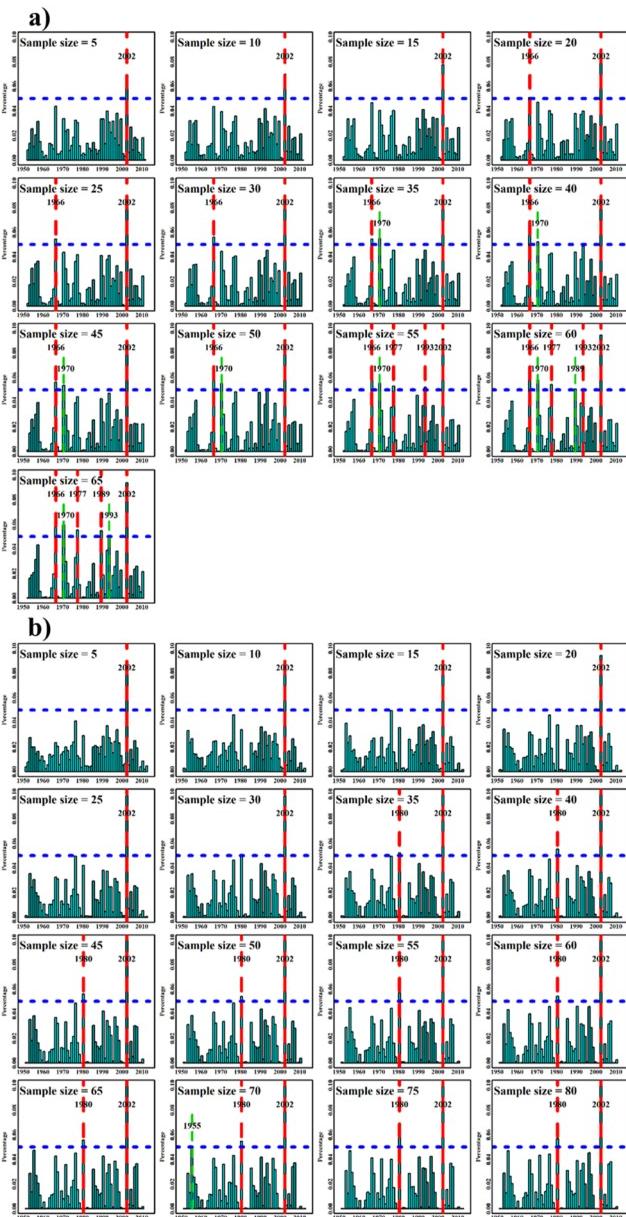


Fig. 5. Chronological cluster analyses results for: (a) The YS catch data and (b) the ECS catch data. Green bars represent probabilities of step-like changes, and red dashed lines indicate time nodes with considerable probability of regime shifts. Blue dashed lines indicate a probability of 0.05, considered a threshold for determining whether a step-like change has occurred. Light green dashed lines represent time nodes with a probability over 0.05 but not regarded as a step change due to its closeness (less than 5 years) to the margin of time series or closeness to another time node of a higher probability. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

dynamics both among the different groups as well as between the YS and ECS (Fig. 12a, b). Gradient forest analyses show that invertebrates have the highest R^2 in the YS and ECS, while the demersal group in the YS and the small pelagic group in the ECS are the groups least well explained by the predictors (Fig. 13a, c). In addition, the analyses identify fishing effort as the most important predictors for the functional groups in the YS and ECS, followed by PC_{evs}. The PC_{ciS} contribute the least to explaining the dynamics of the functional groups in the YS and ECS (Supplement Fig. S10a, c).

The warm- and temperate-water groups are similar for the YS and ECS and they are well fitted with the linearly increasing trends that

likely correspond to consistently rising of fishing effort (Fig. 12c, d). The cold-water group in the YS began decreasing in the mid-1970s and that in the ECS began decreasing in the mid-1960s, but both started to increase again in the late 1980s. Variability in the warm- and temperate-water groups is well explained by predictors with R^2 around 0.9, while the cold-water group is less well explained with R^2 around 0.7 (Fig. 13b, d). Similar to the functional groups, variability in the thermal groups is best explained by fishing effort, followed by PC_{evs} and PC_{ciS} (Supplement Fig. S10b, d).

4. Discussion

4.1. Comparisons of ecosystem structure variability for the YS and ECS

Although we select different taxa to be representative of the YS and ECS regions, there is generally high consistency in pattern variability between the two ecosystems. For example, the gradient forest analyses show that PC_{1,bioS} and PC_{2,bioS} are readily explained by fishing effort, which highlights the importance of this factor in explaining changes in fish catch in both the YS and ECS. Both the YS and ECS PC_{1,bioS} had a decreasing trend starting in the mid-1970s, while the PC_{2,bioS} had an increasing trend prior to the late 1980s that was followed by a decreasing trend. The negative loadings for PC_{1,bioS} and positive loadings for PC_{2,bioS} suggest that the PC_{bioS} represent two types of variability in fish catch. The PC_{1,bioS} are related to species whose catch increased after the late 1970s, including Japanese anchovy (*Engraulis japonicus*, S18) and small yellow croaker (*Larimichthys p.*, S27) in the YS (Supplement Table S1) and hairtail (*Trichiurus j.*, S1) and chub mackerel (*Scomber j.*, S16) in the ECS (Supplement Table S2). The PC_{2,bioS} describe species whose catch peaked in the late 1980s and then collapsed, including Japanese sardine (*Sardinops melanostictus*, S12 in the YS and S18 in the ECS) and silver pomfret (*Pampus argenteus*, S32 in the YS and S41 in the ECS). We note that the increasing trend in hairtail catch in the ECS after the mid-1980s is the opposite to that in Japan, which may be attributed to decreasing fishing effort in Japan since the mid-1980s (Supplement Fig. S2). Therefore, the PC_{bios} in this paper offer only a general review on catch trends and associated temporal variations in ecosystem structure in Chinese waters, while disregarding the Korean and Japanese fisheries, specifically because of the predominance of Chinese catch in the YS and ECS.

Even though the general catch variations in the YS and ECS have similar trends, there are distinguishing patterns in their ecosystem structure dynamics. After the 1950s, high fishing pressure in the YS and ECS led to changes in catch composition that are characterized, in both region, by declines in demersal, high-trophic-level species and rises in pelagic, low-trophic-level species. This has led to decreases in the MTLs in both the YS and ECS (Figs. 3 and 4; Tang, 1987; Cheng et al., 2006). However, the YS MTL started decreasing ten years earlier at a slower rate than the ECS MTL. In addition, the sharp decrease in the ECS MTL in 1975/76 has been partially attributed to the boom in Japanese sardine catch associated with climate change (Tian et al., 2006). After that, the MTLs began to increase in the late 1980s, but the ECS MTL showed a faster recovery than the YS MTL due to a dramatic collapse of sardine (Fig. 4a, b; Watanabe et al., 1995). Up to now, traditional demersal species remain depleted and fishing targets have turned to pelagic species and invertebrates that can consistently sustain considerable yields (Cheng et al., 2006). With respect to the MTC, the pattern in the YS MTC is in accord with subtropical ecosystems, whereas the asymptotic pattern in the ECS MTC is linked more with tropical ecosystems (Cheung et al., 2013). The ECS MTC started increasing ten years earlier than the YS MTC, which corresponded to earlier increase in SST in the ECS than in the YS (Fig. 12c, d). The difference may also be associated with the greater number of tropical (or higher thermal preference) species in the ECS than in the YS, where species have narrower temperatures range and are more sensitive to increasing water temperature (Cheung et al., 2013).

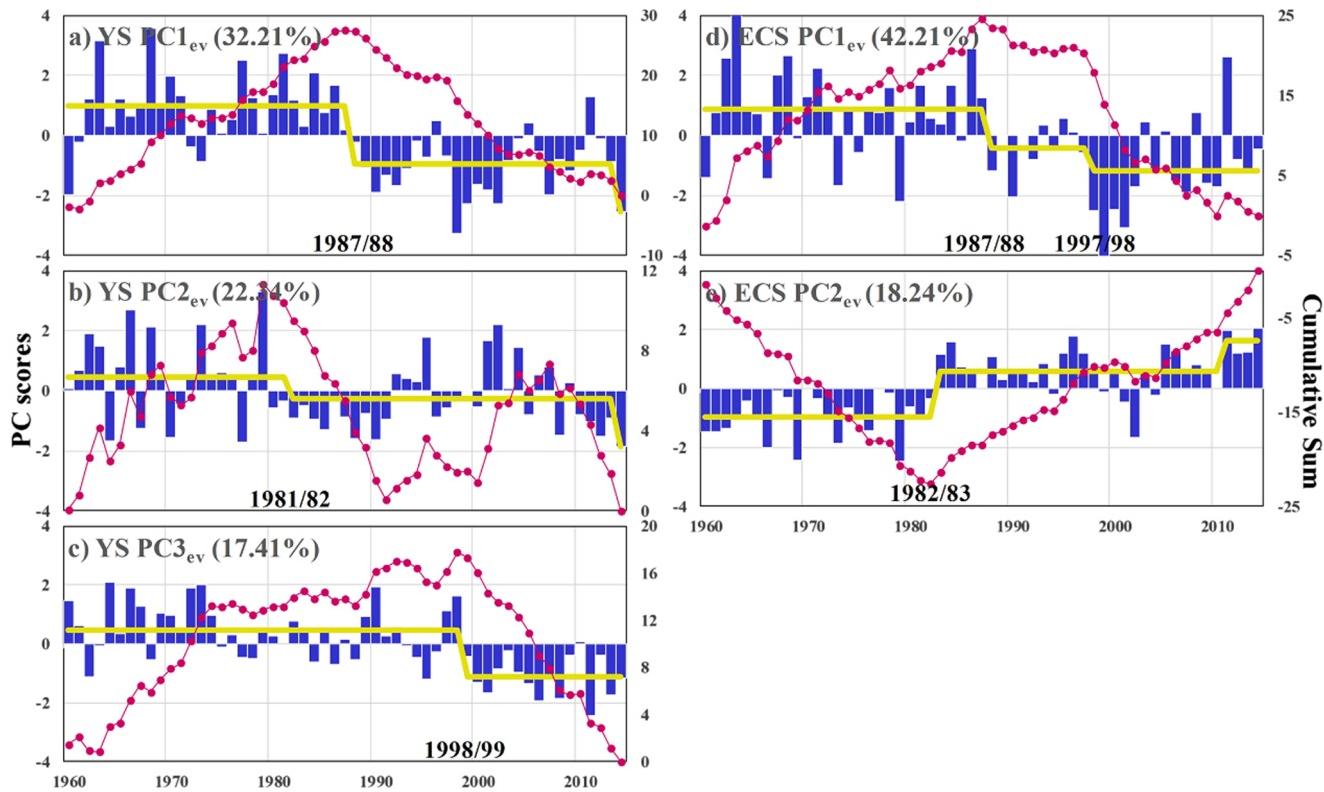


Fig. 6. PC scores for local-scale environmental variables (ev) (a–c) in the YS and (d–e) in the ECS. Blue bars represent scores, red lines with symbols denote cumulative sums for scores and yellow lines denote regime means detected by STARS. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

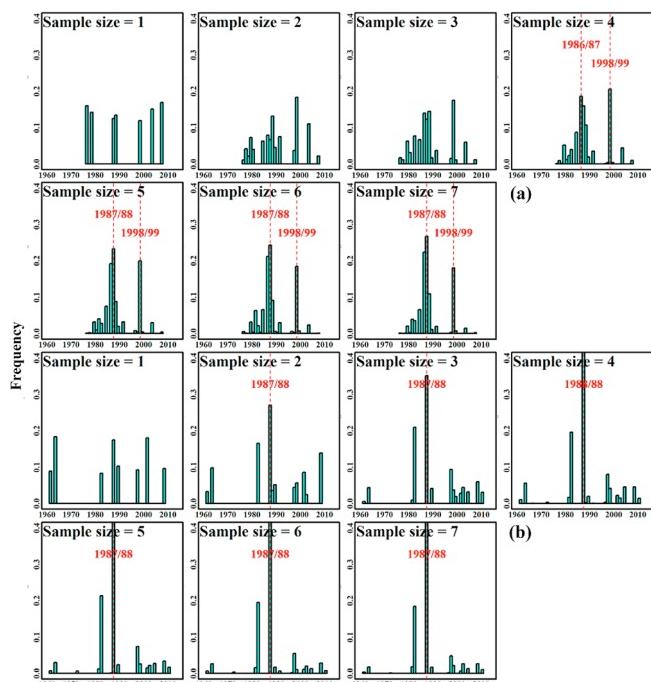


Fig. 7. Chronological cluster results for (a) local-scale environmental variables in the YS and (b) in the ECS. Green bars represent probabilities that regime shifts happen, and red dashed lines indicate time nodes with considerable probability of regime shifts. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

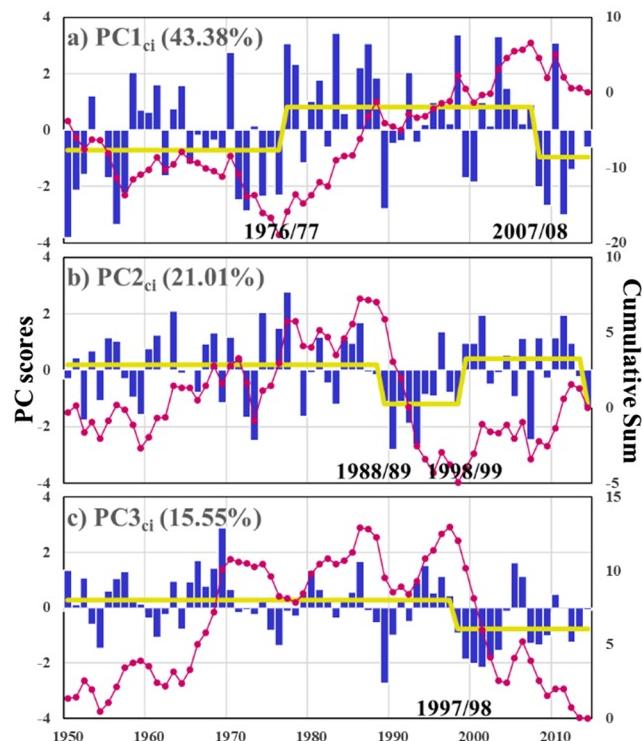


Fig. 8. PC scores for the large-scale climate indices (ci). Blue bars represent scores, red lines with symbols denote cumulative sums for scores and yellow lines represent regime means detected by STARS. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

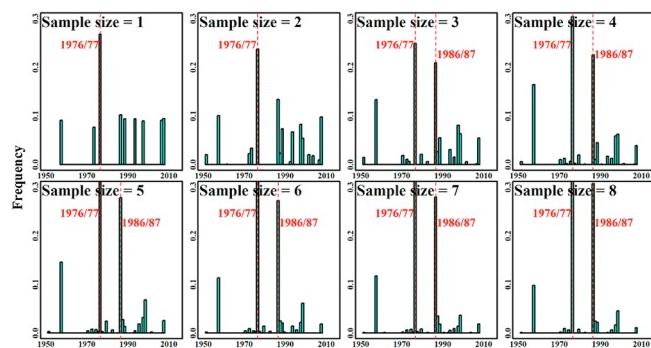


Fig. 9. Chronological cluster results for the large-scale climate indices. Green bars represent probabilities that regime shifts happen, and red dashed lines indicate time nodes with considerable regime shifts probability. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

In this study, different approaches for detecting step-like changes in catch data and regime shifts in environmental variables and climate indices have been employed to help ensure accuracy in the identification of change and shift time nodes. Compared with STARS, which was applied to derived PCs from PCA representing only part of the variances of the data, the MRT with bootstrap (a resampling process used to verify the robustness of results) was a better tool for detecting step-like changes or regime shifts in the multivariate data (Kirkman et al., 2015). However, as a large number of variables are included in our analyses, the MRT results for catch data show less difference between time nodes than those for the environmental variables and climate indices. Therefore, a probability level of 0.05, which is considered a threshold for small probability events, is used as the criterion for determining whether a time node is regarded as a regime shift. The MRT results highlight the decadal variation pattern in the YS, while underline the multi-decadal variation pattern in the ECS. This could be caused by more frequent variations in ocean conditions in the YS compared to the ECS. Because of its geographical location, the YS has less mixed water and, therefore, large vertical temperature gradients, laying the

Table 2

Correlation coefficients between climate indices (ci) / environmental variables (ev) PCs scores and ecosystem surrogates (bio) PCs scores. Single and double asterisks (*) and (**) represent significance levels at $P < 0.05$ and $P < 0.01$, respectively.

PC scores	YS PC1 _{bio}	YS PC2 _{bio}	ECS PC1 _{bio}	ECS PC2 _{bio}
PC1 _{ci}	-0.08	0.29	-0.06	0.33
PC2 _{ci}	0.01	-0.1	0.02	-0.11
PC3 _{ci}	0.32	-0.07	0.31	-0.06
YS PC1 _{ev}	0.56**	0.09		
YS PC2 _{ev}	0.18	-0.12		
YS PC3 _{ev}	0.64**	0.24		
ECS PC1 _{ev}			0.45*	-0.07
ECS PC2 _{ev}			-0.61**	0.13

Table 3

Correlation coefficients among large-scale climate indices (ci) and local-scale environmental variables (ev) PCs scores. Single and double asterisks (*) and (**) represent significance levels at $P < 0.05$ and $P < 0.01$, respectively.

PC scores	YS PC1 _{ev}	YS PC2 _{ev}	YS PC3 _{ev}	ECS PC1 _{ev}	ECS PC2 _{ev}
PC1 _{ci}	0.06	-0.11	0.06	0	0.12
PC2 _{ci}	0.5**	-0.17	-0.34*	0.36*	0.03
PC3 _{ci}	0.56**	0.09	0.11	0.39*	-0.09

Table 4

Correlation coefficients between large-scale climate indices (ci)/local-scale environmental variables (ev) PCs scores and fishing effort (fe). Single and double asterisks (*) and (**) represent significance levels at $P < 0.05$ and $P < 0.01$, respectively.

	PC1 _{ci}	PC2 _{ci}	PC3 _{ci}	YS PC1 _{ev}	YS PC2 _{ev}	YS PC3 _{ev}	ECS PC1 _{ev}	ECS PC2 _{ev}
YS _{fe}	0.08	-0.02	-0.35*	-0.6**	-0.18	-0.61**		
ECS _{fe}	0.07	-0.03	-0.36*				-0.52**	0.6**

Table 1

Time nodes of regime shifts in climate indices (ci)/environmental variables (ev) and step-like changes in ecosystem surrogates (bio). Note that # indicates time nodes that are close to the margin of time-series and should be verified by further data.

Terms		1960s	1970s	1980s	1990s	2000s
Large-scale climate indices	PC1 _{ci}		1976/77			2007/08#
	PC2 _{ci}			1988/89	1998/99	
	PC3 _{ci}				1997/98	
	MRT _{ci}		1976/77	1986/87		
YS environmental variables	YS PC1 _{ev}			1987/88		
	YS PC2 _{ev}			1981/82		
	YS PC3 _{ev}				1998/99	
	MRT _{ev,YS}			1987/88	1998/99	
ECS environmental variables	ECS PC1 _{ev}			1987/88	1997/98	
	ECS PC2 _{ev}			1982/83		
	MRT _{ev,ECS}			1987/88		
YS ecosystem surrogates	YS PC1 _{bio}		1977/78	1989/90	1997/98	
	YS PC2 _{bio}	1966/67	1976/77		1998/97	
	YS MTL	1963/64	1974/75	1985/86	1993/94	
	YS MTC		1976/77		1993/94	
	MRT _{bio,YS}	1966/67	1977/78	1989/90		2002/03
ECS ecosystem surrogates	ECS PC1 _{bio}			1981/82, 1989/90	1996/97	
	ECS PC2 _{bio}	1966/67	1975/76		1998/99	
	ECS MTL		1975/76		1992/93	
	ECS MTC	1966/67	1976/77			2003/04
	MRT _{bio,ECS}			1980/81		2002/03
Summary		Mid-1960s	Mid-1970s	Late 1980s	Late 1990s	Early 2000s

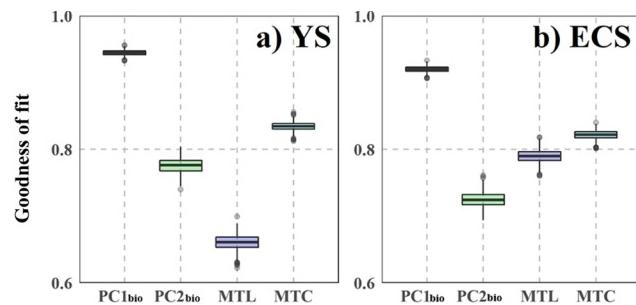


Fig. 10. Model performance (goodness-of-fit R^2) of 1000 runs of the random forests for ecosystem representatives (PC1_{bio} and PC2_{bio}: PC1 and PC2 of catch data, respectively, MTL: mean trophic level, and MTC: mean temperature of catch) in YS (a) and ECS (b).

foundation for more unstable ocean conditions (Sun, 2006). In addition, PCA shows patterns of greater variability in the YS compared to the ECS, and larger variability in mean sea level and water temperature have been observed in the YS than in the ECS, suggesting more drastic and frequent variability in the YS than in the ECS (Fig. 12c, d; Marcos et al., 2012).

4.2. Responses of local-scale environmental change to large-scale climate change

The different ocean conditions in the YS and ECS are directly linked

to the thermal exchange between the atmosphere and the ocean. Ocean conditions in the YS and ECS responded to climate change in the North Pacific in the 1980s, the 1990s and the 2000s with different patterns (Supplement Figs. S11 and S12). In the 1980s, climate conditions in the North Pacific were characterized by a weak winds vortex circulating around the North Pole (negative AOI) and a strong East Asian winter monsoon (positive MOI) forced by a strong Siberian High and a strong Aleutian Low (Supplement Fig. S11; positive SHI and negative NPI in Jung et al., 2017). These processes transported more cold air across polar and high-latitude regions to Chinese waters, directly leading to decreased SST in the YS and ECS due to increased ocean-atmosphere heat exchange (Supplement Fig. S12).

In the 1990s, a strong Arctic Oscillation associated with a strong winds vortex that confined cold air invaded the south effectively. A weak East Asian winter monsoon (negative MOI) forced by a weak Siberian High, a weak Aleutian Low and frequent El Niño events (negative SOI) that produced high sea level pressure in the Western Pacific Warm Pool (Supplement Fig. S11; negative SHI and positive NPI in Jung et al., 2017), which brought less cold air to the south, resulting in warm air and water temperature in the YS and ECS (Supplement Fig. S12). Moreover, frequent El Niño events during this period resulted in the rising water temperatures in Niño 4 region (decreasing SOI and increasing Niño 4) and may have indirectly caused elevated water temperature in the YS and ECS (Jin et al., 2013).

In the 2000s, climate change in the North Pacific featured by an intermediate intensity Arctic Oscillation and East Asian winter monsoon forced by a weak Siberian High but an intermediate Aleutian Low and frequent La Niña events that, in turn, resulted in low sea level

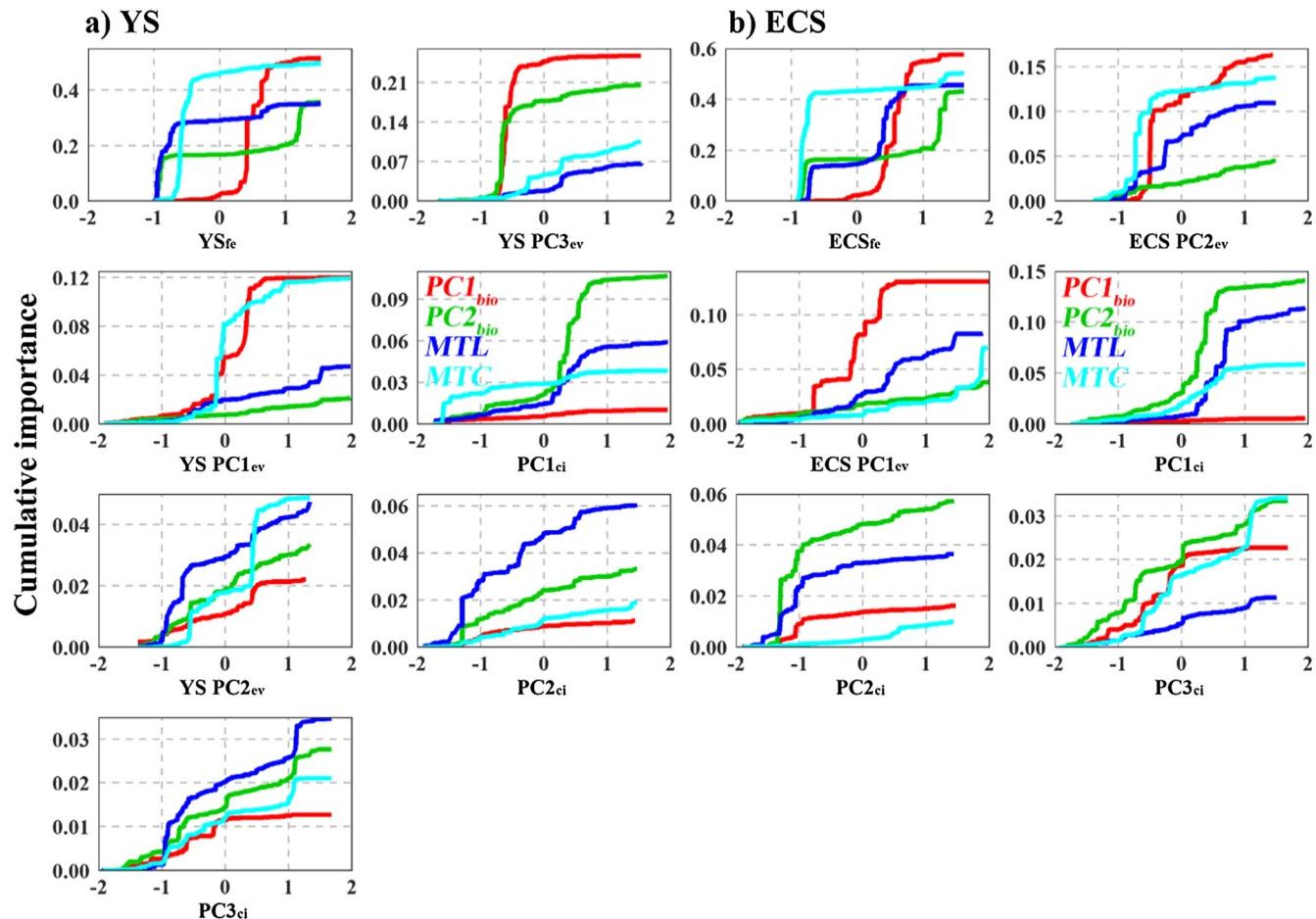


Fig. 11. Cumulative shifts (in R^2 units) of ecosystem representatives (PC1_{bio} and PC2_{bio}: PC1 and PC2 of catch data, respectively, MTL: mean trophic level, and MTC: mean temperature of catch) in YS (a) and ECS (b) in response to the fishing effort (fe), local-scale environmental variables (ev) and large-scale climate indices (ci).

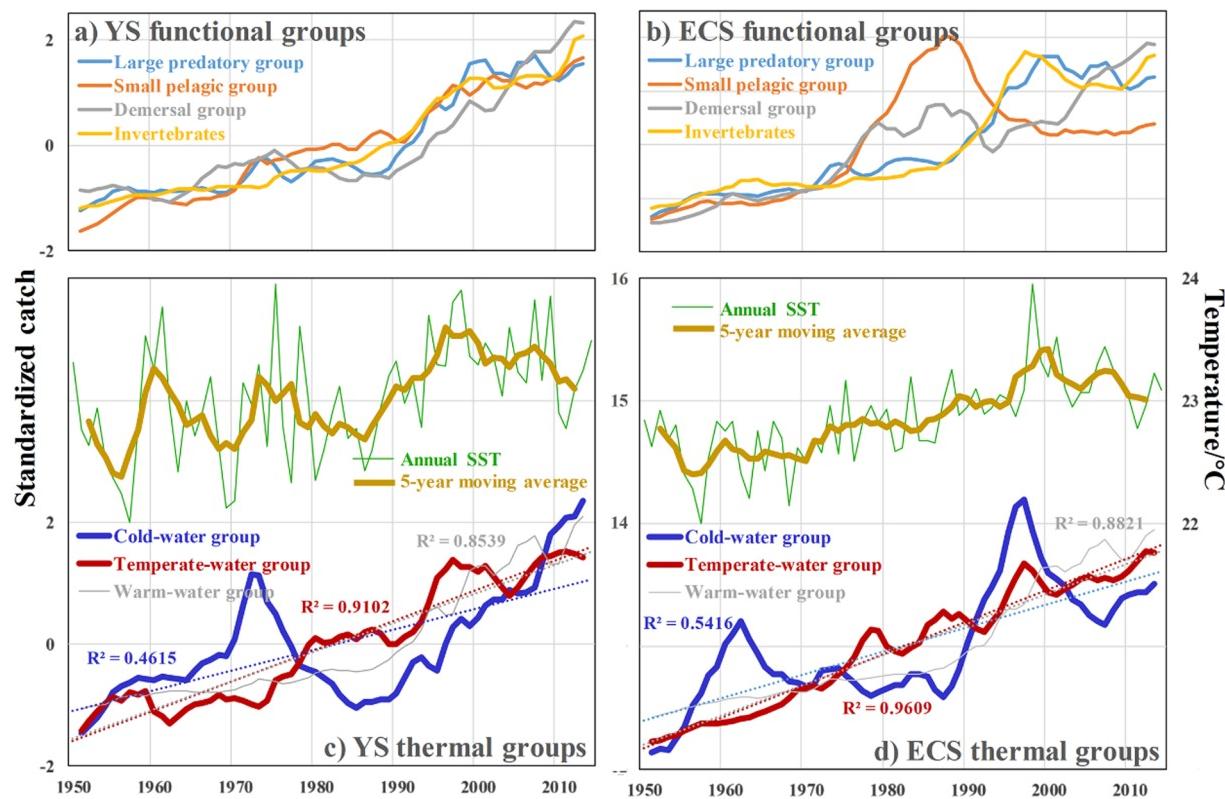


Fig. 12. Three-year moving average trends in: (a) The YS functional groups; (b) the ECS functional groups; (c) the YS thermal groups and (d) the ECS thermal groups. Annual SSTs in the YS and ECS and their five-year moving averages are added to panel c and d, respectively. Linear trends are fitted to the thermal groups in the YS (c) and ECS (d).

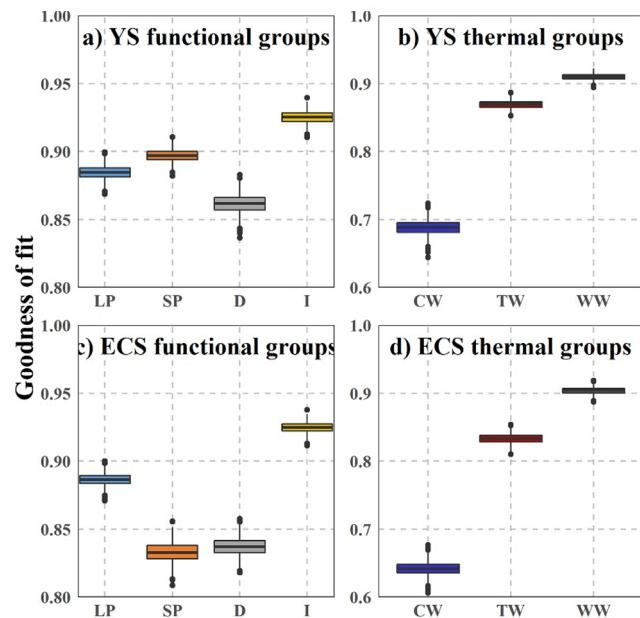


Fig. 13. Model performance (goodness-of-fit R^2) of 1000 runs of the random forests for functional groups (LP: large predatory group, SP: small pelagic group, D: demersal group and I: invertebrates) in the YS (a) and ECS (c) as well as for thermal groups (CW: cold-water, TW: temperate-water and WW: warm-water group) in the YS (b) and ECS (d).

pressure in the Western Pacific Warm Pool, which brought moderately cold air to the south (Supplement Fig. S11). However, the YS and ECS showed different response patterns to the changing climate conditions. Moderately cold air from the north led to cold air and water temperature in the YS, but this effect was insufficient to decrease air and water

temperature in the ECS. Consequently, the ECS was still in a warm regime in the 2000s (Supplement Fig. S12). In addition, an intermediate Arctic Oscillation, together with an intermediate East Asian winter monsoon, transported moderately dry air from the north to the south, which resulted in decreased precipitable water content in the YS but not in the ECS. Beyond that, the surface wind in the YS turned from being northwestward to westward from the 1990s to the 2000s, which coincided with the intermediate Arctic Oscillation and East Asian winter monsoon (Fig. 6; Supplement Fig. S8).

4.3. Responses of ecosystem structure, and functional and thermal groups to physical drivers

The YS and ECS PC_{1bio}s, which are highly representative of ecosystem structure, show step-like changes that are synchronous with regime shifts in the environment and are possibly explained by physical drivers. Considering the high correlation between the YS and ECS PC_{1bio}s, it is possible that the YS PC_{1bio}s achieve higher correlation with the ECS PC_{1bio}s, and vice versa. To be sensible ecologically, we only associate PC_{1bio}s with PC_{1env}s of the same ecosystem in both the correlation analyses and the gradient forest analyses.

As the PC_{1bio}s are highly correlated with fishing effort, it has been challenging to distinguish the effects of physical drivers from those of fishing effort. In addition, the dependence between physical drivers and fishing effort make the identification of climate-induced variations in ecosystem structure in Chinese waters more difficult, which also suggests that simple correlation analyses are of limited value in Chinese waters, as well as in other exploited ecosystems. However, threshold responses of the PC_{1bio}s to the PC_{1env}s based on the gradient forest analyses highlight the role of environmental change in the dynamics of ecosystem structure (Fig. 11). By contrast, the MTLs are relatively poorly explained by fishing effort and physical drivers in the gradient forest analyses (Fig. 10). The MTL has been extensively used to measure

sustainability in exploited marine ecosystems and to determine whether fishing-down the food chain has occurred (e.g. Bhathal and Pauly, 2008; Hermida and Delgado, 2016). However, our results showed that variations in the YS and ECS MTLs could not be explained directly by changes in fishing effort, which roughly correspond to a linear increase, particularly in the 1990s when greatly increased fishing effort coincided with increases in the YS and ECS MTLs (Fig. 4a, b). On the contrary, variations in the MTLs may be largely affected by climate change, such as the booming of *S. melanostictus* in the 1980s in the ECS that caused a sharp decline in the ECS MTL followed by dramatic recovery in the 1990s, which was similar to the results in Sea of Japan (Tian et al., 2006). Therefore, the MTL could serve as an effective indicator of climate-induced variability rather than fishing-induced variability in ecosystem structure in Chinese waters. In addition, variations in the YS and ECS MTCs deliver significant warming signals in catch and are in accord with the warming in atmospheric and oceanic conditions, indicating the validity of using the MTC to explore the climate-induced dynamics of ecosystem structure.

The functional and thermal groups, with their different biological characteristics, show significant spatial-temporal differences in their responses to local-scale environmental changes. The large predatory groups in the YS and ECS were well explained by variations in fishing effort, but they responded weakly to physical drivers (Fig. 12). In general, taxa in the large predatory group are strong swimmers and have extensive migration spaces (Svendsen et al., 2016). The commonly reported responses of this group to environmental changes are declines in body size and habitat distribution shifts (Genner et al., 2010; Robinson et al., 2015). Although they exhibited stable catch proportion and high resistance to external environmental changes, they may have experienced changes in life histories and distributions that were not reflected in our research. The small pelagic groups showed distinct responses to environmental changes between the YS and ECS (Fig. 12a, b). The small pelagic groups were supposed to be largely affected by physical drivers because of their specific biological characteristics. Another research of ours that focused on the responses of six individual small pelagic species to environmental changes found different patterns among them (Ma et al., 2018). Therefore, the lack of environmental effects on the small pelagic groups in the YS and ECS may result from the neutralization of different species-specific patterns of response to environmental changes, which is consistent with previous research (Griffith et al., 2018). Moreover, the response of the small pelagic group in the ECS is dominated by *S. melanostictus*, which underwent an extreme increase and subsequent collapse (Yasuda et al., 1999; Tian et al., 2006). The demersal group in the YS responded weakly to environmental changes, while that in the ECS showed considerable responses to environmental changes. Unlike the small pelagic groups, the demersal groups are reported to have collective responses to environmental changes (Griffith et al., 2018). However, with the various optimal ocean conditions for the different aggregated species, it is difficult to assess the environmental changes mechanism impacting catch variations in the demersal groups.

Thermal variations are of importance to thermal groups with their high sensitivity and direct responses to changing water temperature (Burt et al., 2011; O'Gorman et al., 2016). There is little doubt that the cold-water groups in both the YS and ECS suffered the most from the increasing water temperature (high amplitude and low R^2 in Fig. 12c, d). Catch of the cold-water group in the YS began decreasing in the mid-1970s and it in the ECS began decreasing in the mid-1960s, and both started to increase again in the late 1980s. Decreasing catch with increasing fishing effort and increasing water temperature may send a signal that the cold-water group is undergoing unfavorable climatic conditions. In addition, increasing catch with increasing fishing effort and increasing water temperature indicates the more powerful effects of fishing than climatic conditions. Contrary to the cold-water group, the warm- and temperate-water groups exhibited high resistance to environmental changes and their trends were largely determined by the

increased fishing effort (low amplitude and high R^2 in Fig. 12c, d). Particularly in the YS, past thermal variability (SST increased from below 15 °C to over 15 °C) had negligible impact on the warm-water taxa due to their high optimal temperature (median over 25 °C).

The different responses of the thermal groups to environmental changes could be interpreted as differences in their life history characteristics. Tian et al. (2011) illustrated the possible mechanism of ocean conditions impacting thermal groups as a result of variations in water temperature affecting the reproduction and recruitment of marine life, which is supported by our results.

It is worth noting that the functional and thermal groups in the ECS display larger amplitude variability than those in the YS (Fig. 12), which indicates that environmental changes have more powerful effects on the ecosystem structure of the ECS compared to the YS. While the YS is featured by relatively short-term, high-frequency variations in ocean conditions, the ECS is characterized by relatively long-term, low-frequency variations (Sun, 2006; Marcos et al., 2012), resulting in more effective impacts on the ecosystem structure. This is in accord with the “pulse-press” theory states that ecologically important shifts are characterized by a sharp peak in environmental variability (i.e., a strong pulse disturbance/shift event) followed by lower variability that maintains post-shift conditions (i.e., a persistent press disturbance) (Litzow and Mueter, 2014). Moreover, the relatively chronic climatic disturbance in the ECS gradually degrades the original ecosystem, making the ecosystem less resilient to future climatic disturbances, resulting in more significant ecosystem reorganization (Cote and Darling, 2010).

4.4. Effects of fishing and implications for fishery management

Despite considerable effects of climate change, fishing is still an important forcing factor for variations in marine ecosystem structure (Last et al., 2011). With catch data being used to indicate ecosystem structure in this study, the quality of these data is vital for ensuring the validity of our research. Although there is a concern for potential overestimation of Chinese catch in the YS and ECS due to the observed drastic catch increase in the 1980s and 1990s, and also has been maintained since 2000, this concern is irrelevant to this study for three main reasons: (1) Chinese fishing effort increased dramatically in the 1980s and 1990s with more efficient fishing rates and expanded fishing grounds and has remained stable since the 2000s (Kang et al., 2018), which corresponds well with the increase in Chinese catch reconstructed by Sea Around Us, suggesting the reliability of the portrayed catch increase. In addition, Szuwalski et al. (2017) reported that “ecosystem engineering” (i.e., intense fishing on large fish, which subsequently causes an increase in the productivity of smaller fish) was feasible for Chinese fisheries, indicating the high level in catch since 2000 was also realistic due to the implementation of this process; (2) Chinese catch data from the Sea Around Us, intended to benefit aggregated, long-term and global- or regional-scale research, are lower than the reported catch, which would mitigate the over-inflation in Chinese catch (Watson and Pauly, 2001; Pauly and Zeller, 2016); (3) most importantly, our research focuses on the long-term variability in marine ecosystem structure rather than on absolute catches of specific species in some fixed years.

Isolating the effects of climate versus fishing on ecosystems is clearly very challenging, especially for the present case, where we used catch data to describe ecosystem structure. Intensive step changes in ecosystem surrogates were observed in the mid-1960s but no regime shifts were detected in the large-scale climate indices or local-scale environmental variables (Table 1). Japanese demersal trawl fishery targeting demersal species and purse-seine fishery targeting pelagic species flourished in the YS and ECS in the 1960s (Otaki, 1993; Cheng et al., 2006; Supplement Fig. S2). Meanwhile, Korean fisheries largely increased fishing effort for demersal species, resulting in heavily fished major stocks in the YS (Zhang et al., 2014), which may contribute to the

step-like change in the YS MTL in the mid-1960s. However, stability in the ECS MTL and step-like change in the ECS MTC in the mid-1960s appear to be induced by environmental factors, such as increasing temperature rather than fishing effort, which can be verified by further research. Widespread step-like changes occurred in ecosystem surrogates in the mid-1970s, corresponding to the most well-known climatic regime shifts in the North Pacific (Wu et al., 2005; Overland et al., 2008; Xie et al., 2010). No obvious shifts in surrogates for environmental variables were detected in the 1970s. On the one hand, this may be caused by the PCA that only captures part of variance of the raw environmental variable data and fails to exhibit variation pattern in the 1970s. For example, sea level pressure in the YS had a step-like change around 1976/77 that was not shown by YS PC2_{ev}. On the other hand, it may be caused by incomplete descriptions of local-scale environmental changes (only 7 variables were included in our research). For instance, the volume of the Kuroshio had a great increase in the 1976/77 (Zhang et al., 2000), which would have effects on environmental change in the ECS but was not reflected by our selected environmental variables. In addition, teleconnection could contribute to variability in local-scale environmental changes, which would also have great ecological importance. During this same period, Japanese fishing effort was steadily lower than the previous period, while Korean fishing effort greatly increased (Zhang et al., 2014). Based on the above findings, we infer that increasing fishing effort in the YS in the 1970s, in tandem with climatic regime shifts, altered the YS ecosystem structure, while step-like changes in the ECS in the mid-1970s were more likely linked to a climatic regime shift (Tian et al., 2006).

The fishing effort index in the YS and ECS employed in this study was represented by standardized Chinese fishing boats engine power due to the lack of other supporting data. This index may have underestimated fishing effort by not including those of other fishing countries, such as Japan and Korea. Nevertheless, the PC1_{bios} show marked correlations with engine power time series, indicating the dominance of Chinese fishing efforts in Chinese waters (Supplement Table S5). In addition, catches in the YS and ECS by China, Japan and Korea (north and south) also reveal the leading role of the Chinese fishery (Supplement Fig. S13), providing the validity for using Chinese fishing effort. In addition, variations in marine ecosystem structure consist of complicated multi-factor processes that are forced by integrated effects of not only climate change and fishing but also anthropogenic activities and biological interactions (Aberhan et al., 2006; Möllmann et al., 2009; Wu et al., 2017). Therefore, better understanding of the effects of anthropogenic activities on marine ecosystems and more accurate evaluation of intra- and inter-species relationships would be beneficial for research on marine ecosystem structure.

Variations in fishing effort and climate change interact with each other, intensifying variations in marine ecosystem structure (Tian et al., 2011). Fishing pressures may be different among the different functional and thermal groups under the same climate conditions and the same fishing effort due to their diverse responses to climate change. Even for the same group, fishing pressure can be different under different climate conditions but the same fishing effort. Fishing pressure can be intensified by unfavorable climate conditions even under declining fishing effort (Tian, 2009; Tian et al., 2012). Therefore, it is important to identify the response of ecosystem structure to climate change before evaluating fishing impacts and implementing corresponding fishery management strategies.

Current fishery management strategies in Chinese waters do not account for the role of climate change in marine ecosystem dynamics. Our results indicated that variations in ecosystem structure in Chinese waters are affected by climate change. Consequently, fishery management in Chinese waters should take into full consideration future climate change and adapt fishing effort in a timely manner to mitigate the negative effects of unfavorable climate conditions.

With the predicted continual warming in the future, global fishes and fisheries will encounter great challenges (Cheung et al., 2016;

Rogelj et al., 2016). Small pelagic species and demersal species all respond to climate change but in different ways with small pelagic species responding at individual level and demersal species responding as a cohort. This calls for fishery management strategies aimed at individual species for small pelagic fisheries and at assemblages for demersal fisheries. In addition, our results and those of other studies demonstrate that cold-water species will suffer more and even face the risk of collapse from increasing water temperature and constant or intensive fishing effort (Tian et al., 2008, 2013a). Due to unfavorable climate conditions in the future, cold-water species fisheries should be managed with greater cautions in order to maintain sustainable exploitation. Warm-water species on the other hand may potentially benefit from global warming. However, the benefit of global warming to the entire ecosystem is less certain. Because of the diverse biological characteristics of these warm-water species, some of them are likely to bloom, causing other species and the whole ecosystems to be disrupted through interspecific competition, top-down and bottom-up effects (Ware and Thomson, 2005; Suryan et al., 2006). Therefore, it is important that fisheries management take into account the different responses of marine organisms to future climate change.

5. Conclusions

The ecosystem structure of the Yellow Sea (YS) and East China Sea (ECS) are characterized by marked decadal-scale variability with step-like changes in structure in the mid-1960s, the mid-1970s, the late 1980s and the late 1990s. These changes closely correspond with climatic regime shifts in the mid-1970s, the late 1980s and the late 1990s. For both the YS and ECS, the first principal components of the catch data are best explained by fishing effort in tandem with physical drivers. The mean trophic level and mean temperature of catch are largely affected by climate change and may be used as indicators to effectively explore climate-induced variations in ecosystem structure. The functional and thermal groups show strong linkages with fishing effort and with physical drivers, particularly local-scale environmental variables. Results highlight the importance of fishing and the validity of biological grouping in future investigations of environmental impacts on marine organisms. The cold-water group was most impacted by increasing water temperature in both the YS and ECS, while the warm-water group was little affected by existing ocean thermal conditions in the YS. “Atmosphere-ocean-ecosystem” processes effectively explain the ecosystem structure dynamics of the YS and ECS, and may serve as a framework for understanding climate-forcing dynamics in marine ecosystems in other regions. Future fishery and ecosystem management should take into consideration the effects of climate change on marine organisms, especially for cold-water species. Research on the response patterns for both individual and collective marine organisms to climate change are of critical importance for formulating proper management strategies.

Declarations of interest

None.

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Appendix A. Supplementary material

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.pocean.2019.04.008>.

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